NOTES ON THE DISARTICULATION OF *XYLOTHAMIA* (ASTERACEAE: ASTEREAE)

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ABSTRACT

The genus *Xylothamia*, primarily of the Chihuahuan and Sonoran deserts in northern Mexico, was originally described with nine species. Molecular evidence by Urbatsch et al. has subsequently shown that these species form two separate clades. Among species in each of the two groups, details of phylogenetic position vary, depending on optimality criteria used in the analysis. Four species of *Xylothamia*, including the type, are most closely related to the Caribbean genus *Gundlachia* and were transferred to *Gundlachia* by Urbatsch and Roberts. These four, however, can be interpreted as having a sister relationship with *Gundlachia* and are here maintained within *Xylothamia*. The remaining five species of *Xylothamia* are part of a clade that includes *Amphiachyris*, *Bigelowia*, *Euthamia*, *Gutierrezia*, *Gymnosperma,* and *Thurovia*. Molecular evidence indicates that two of the five species have a sister relationship but that neither this pair nor any of the other three are unambiguously closely related to any established genus. Segregates were proposed for these five species by Urbatsch and Roberts as the ditypic genus *Neonesomia* and the monotypic genera *Chihuahuana*, *Medranoa*, and *Xylovirgata*. In contrast, morphological features and geographic proximity within the Chihuahuan Desert justify congeneric treatment for these five species, which are here united in *Medranoa* (with *Chihuahuana*, *Neonesomia*, and *Xylovirgata* placed in synonymy). New combinations are **Medranoa johnstonii** (G.L. Nesom) G.L. Nesom, comb. nov., **Medranoa palmeri** (A. Gray) G.L. Nesom, comb. nov., **Medranoa purpusii** (Brandeg.) G.L. Nesom, comb. nov., and **Medranoa pseudobaccharis** (S.F. Blake) G.L. Nesom, comb. nov.

RESUMEN

El género *Xylothamia*, de distribución primaria en los desiertos de Chihuahua y Sonora del norte de México, se describió originariamente con nueve especies. Los datos moleculares de Urbatsch et al. han mostrado que estas especies forman dos clados separados. Entre las especies de cada uno de los grupos, varían los detalles de posición filogenética, dependiendo de los criterios de optimización usados en el análisis. Cuatro especies de *Xylothamia*, que incluyen el tipo, están más cercanamente relacionadas con el género caribeño *Gundlachia* y fueron transferidas a *Gundlachia* por Urbatsch y Roberts. Estas cuatro, sin embargo, pueden interpretarse como el grupo hermano de *Gundlachia* y se mantienen aquí en *Xylothamia*. Las restantes cinco especies de *Xylothamia* son parte de un clado que incluye *Amphiachyris*, *Bigelowia*, *Euthamia*, *Gutierrezia*, *Gymnosperma,* y *Thurovia*. Las pruebas moleculares indican que dos de estas cinco especies tienen una relación de grupo hermano pero que ni este par ni ninguna de las otras tres están fuertemente relacionadas con ningún otro género establecido. Se han propuesto segregaciones de estas cinco especies por Urbatsch y Roberts como género ditípico *Neonesomia* y los géneros monotípicos *Chihuahuana*, *Medranoa*, and *Xylovirgata*. En contraste, las características morfológicas y la proximidad geográfica en el desierto de Chihuahua justifica el tratamiento congenérico de estas cinco especies, dque se unen aquí en *Medranoa* (con *Chihuahuana*, *Neonesomia*, y *Xylovirgata* colocadas en la sinonimia). Las nuevas combinaciones son **Medranoa johnstonii** (G.L. Nesom) G.L. Nesom, comb. nov., **Medranoa palmeri** (A. Gray) G.L. Nesom, comb. nov., **Medranoa purpusii** (Brandeg.) G.L. Nesom, comb. nov., y **Medranoa pseudobaccharis** (S.F. Blake) G.L. Nesom, comb. nov.

The genus *Xylothamia* was proposed to include eight species (Nesom et al. 1990) traditionally associated with *Ericameria*. A ninth was added soon after (Nesom 1992). Except for *Xylothamia diffusa*, which occurs in Sonora, Baja California, and Baja California Sur, all are species of the Chihuahuan Desert. Molecular evidence by Urbatsch et al. (2003) subsequently indicated that the nine species of *Xylothamia* form two separate clades. Four species, including the type, are most closely related to the Caribbean genus *Gundlachia* (sensu Lane 1996). The remaining five species are part of a clade that includes *Amphiachyris*, *Bigelowia*, *Euthamia*, *Gutierrezia*, *Gymnosperma,* and *Thurovia*. *Gundlachia* and its related *Xylothamia* species are sister to the other group, and this larger clade is essentially what has been termed the "Gutierrezia group" (e.g., Nesom 2000).

Parsimony analyses by Urbatsch et al. were based on combined data sets of the external transcribed spacer (ETS) and internal transcribed spacer (ITS) DNA sequences, both with and without indels. A morphological data set including ten characters was added in some of the analyses. The biphyletic nature of

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Xylothamia is clear, but among species in each of the two lineages, details of phylogenetic positions vary, depending on which optimality criterion was used in the analysis.

Taxonomy proposed by Urbatsch and Roberts (2004) merged the four species of *Xylothamia* sensu stricto with *Gundlachia*. The other five *Xylothamia* species were apportioned into four new genera. The comments below propose a taxonomic alternative for the species of these two groups and the taxonomic summary shows how the original nine species of *Xylothamia* will be treated in the Astereae of Mexico (Nesom, expected 2007).

Expanded *Gundlachia*

The four species of *Xylothamia* sensu stricto and *Gundlachia* are shown by Urbatsch et al. (2003) as sister groups in analyses including indels (Figs. 1A, a ratchet analysis, and 1B, a heuristic analysis), in a Bayesian analysis (Fig. 2), and in a heuristic analysis including indel data and the morphological character matrix (Fig. 3, right side). *Xylothamia riskindii*, the other three *Xylothamia* species, and *Gundlachia* are shown as an unresolved trifurcation in a bootstrap analysis including indel data and a morphological character matrix (Fig. 3, left side). The four *Xylothamia* species are shown as a basal grade to *Gundlachia* in a tree derived from a ratchet analysis of the molecular data excluding indels (Urbatsch et al. 2003, Fig. 4). The topology shown by Urbatsch and Roberts (2004, Fig. 1) was based on the earlier-published Figure 4.

A close relationship of Caribbean *Gundlachia* to Mexican *Xylothamia* sensu stricto is supported by the molecular analyses, but the topology of the relationship is not resolved. Morphology of Caribbean *Gundlachia* is distinctive and relatively consistent among the taxa, and the geographical and morphological contrasts (noted below) with *Xylothamia* provide a rationale for recognition of these two species groups as separate genera. *Gundlachia* is paraphyletic without *Xylothamia* in only one of the various analyses by Urbatsch et al.

Urbatsch and Roberts (2004, p. 250) noted that "Flagelliform trichomes having a subterminal appendage attachment characterize the Caribbean species [of *Gundlachia*] and similar trichomes are seen in *G. riskindii*." Caribbean *Gundlachia* and "*Gundlachia*" *riskindii* also have laminar, spatulate leaves. Neither of these similarities, however, appears to have significantly influenced the parsimony analyses that included morphological data. Nesom et al. (1990, p. 103) emphasized the irregularly lobed disc corollas found in all nine of the *Xylothamia* species, unique among all their potentially close relatives, including *Gundlachia*: "The zygomorphic disc corollas of [all of the *Xylothamia*] species are even more remarkable, because to our knowledge, they do not occur in any other North American Astereae. Typically, two of the sinuses are cut nearly to the base of the throat, one is very shallow, and the other two are intermediate in depth. The two lobes on either side of the shallow sinus are erect, but the other three are sharply reflexed to coiling." This feature was not included in the morphological analysis by Urbatsch et al. (2003); it was noted by Urbatsch and Roberts (2004) as a feature of all of the original nine *Xylothamia* species, but it was not mentioned as a synapomorphy.

Xylothamia riskindii is disparate among the four species considered here as *Xylothamia* sensu stricto, as evidenced by the following contrast.

1. Leaves flat, obovate-spatulate; heads solitary; ray florets 7–13; involucres 7–8 mm diam.; disc florets 30–50 _____ **X. riskindii**

1. Leaves involute, appearing terete; heads in loose or compact cymes or sessile in groups of 2–3 at branch apices; ray florets 0 or 1–3 hidden within the involucre; involucres 2.5–4 mm diam.; disc florets 3–7_____ **X. diffusa, X. triantha,** and **X. truncata**

It also is distinct in comparison to taxa of *Gundlachia*.

1. Subshrubs ca 8–15 cm tall; heads solitary, sessile to subsessile; involucres broadly turbinate, 7–8 mm diam.; phyllaries without orange-resinous midveins; ray florets 7–13, corollas yellow; disc florets 30–50 _____ **X. riskindii**

1. Shrubs to 200 cm tall; heads in clusters of 1–5, the clusters in racemes or corymbs, in turn borne in panicles or flat-topped to slightly rounded corymboid clusters; involucres cylindric to narrowly obconic, 2–4 mm diam.; phyllaries with orange-resinous midveins; ray florets 3–8, corollas white; disc florets 3–10 _____**Gundlachia**

Urbatsch and Roberts (2004, p. 250) noted that certain evidence suggests that "*G. riskindii* may represent the ancestral state for *Gundlachia* or may be a link connecting the Caribbean and the Mexican species." In the evaluation here, *Xylothamia riskindii* remains unusual among the species placed in *Xylothamia*.

Chihuahuana, *Medranoa*, *Neonesomia*, and *Xylovirgata*

Urbatsch and Roberts (2004, p. 244) noted that "With regard to the other five species of *Xylothamia*, *X. johnstonii*, and *X. palmeri* constitute a robustly supported clade (Urbatsch et al. 2003) that is herein proposed as the new genus *Neonesomia*. The three remaining species of *Xylothamia* are each treated as monotypic genera [*Chihuahuana*, *Medranoa*, and *Xylovirgata*] because they are not unambiguously supported as monophyletic or placed within existing genera based on DNA sequence data (Urbatsch et al. 2003), and they are each morphologically unique."

In molecular analyses including indels (Urbatsch et al. 2003: Figs. 1A, a ratchet analysis, and 1B, a heuristic analysis), *Chihuahuana*, *Medranoa*, and *Xylovirgata* constitute a monophyletic group and *Neonesomia* is basal to the clade that includes the three other new genera above and six more (*Amphiachyris*, *Bigelowia*, *Euthamia*, *Gutierrezia*, *Gymnosperma,* and *Thurovia*). In the Bayesian analysis (Fig. 2), *Medranoa* and *Chihuahuana* have a sister relationship and *Neonesomia* is most closely related to *Thurovia*. In analyses including indel data and the morphological character matrix, the position of all four new genera is unresolved (Fig. 3, left side-bootstrap) or *Medranoa* and *Xylovirgata* show a sister relationship (Fig. 3, right side-heuristic). In a ratchet-derived consensus tree resulting from an analysis excluding indels (Fig. 4), the positions of *Neonesomia* and *Medranoa* are unresolved, while *Chihuahuana* and *Xylovirgata* are sister taxa.

While it is clear that each of the four taxa treated as a new genus by Urbatsch and Roberts is morphologically unique and that the molecular analyses do not provide unambiguous phyletic resolution for them (apart from their separation from *Xylothamia* sensu stricto), molecular data do not provide a compelling rationale to recognize four new genera among five species of the Chihuahuan Desert. Analogous to the position of *X. riskindii* among its three congeners, *X. purpusii* (below as *Medranoa purpusii*) is relatively more distinctive in morphology and on that basis might justifiably be treated as a monotypic genus apart from its four congeners. Treatment of these species within a single genus is at least as justified, based on current evidence, as is their distribution among four. Geography and morphology provide support for their recognition as a single lineage: geographic proximity commonly is an indicator of close evolutionary relationship, and the zygomorphic disc corollas (discussed above) in this group of five species provide a potential apomorphy that suggests common ancestry, as in the original delimitation of *Xylothamia*. While it cannot be definitively argued that the previous treatment is flawed, a more parsimonious and conservative taxonomy is favored here.

TAXONOMIC SUMMARY

XYLOTHAMIA Nesom, Suh, Morgan & Simpson, Sida 14:106. 1990. TYPE SPECIES: *Xylothamia (Aplopappus) triantha* (S.F. Blake) G.L. Nesom.

1. Xylothamia diffusa (Benth.) G.L. Nesom, Sida 14:109. 1990. *Ericameria diffusa* Benth.; *Gundlachia diffusa* (Benth.) Urbatsch & R.P. Roberts.

2. Xylothamia triantha (S.F. Blake) G.L. Nesom, Sida 14:113. 1990. *Aplopappus [Haplopappus] trianthus* S.F. Blake; *Ericameria triantha* (S.F. Blake) Shinners; *Gundlachia triantha* (S.F. Blake) Urbatsch & R.P. Roberts.

3. Xylothamia riskindii (B.L. Turner & G. Langford) G.L. Nesom, Sida 14:113. 1990. *Ericameria riskindii* B.L. Turner & G. Langford; *Gundlachia riskindii* (B.L. Turner & G. Langford) Urbatsch & R.P. Roberts.

4. Xylothamia truncata G.L. Nesom, Phytologia 73:318. 1992. *Gundlachia truncata* (G.L. Nesom) Urbatsch & R.P. Roberts.

MEDRANOA Urbatsch & R.P. Roberts, Sida 21:254. 2004. TYPE SPECIES: *Medranoa (Ericameria) parrasana* (S.F. Blake) Urbatsch & R.P. Roberts.

Chihuahuana Urbatsch & R.P. Roberts. TYPE SPECIES: *Chihuahuana* (*Ericameria*) *purpusii* (Brandeg.) Urbatsch & R.P. Roberts.

Neonesomia Urbatsch & R.P. Roberts. TYPE SPECIES: *Neonesomia* (Aster) *palmeri* (A. Gray) Urbatsch & R.P. Roberts.

Xylovirgata Urbatsch & R.P. Roberts. TYPE SPECIES: *Xylovirgata* (*Haplopapus*) *pseudobaccharis* (S.F. Blake) Urbatsch & R.P. Roberts.

Etymology.—Medranoa is chosen here, from among the four possibilities, as the name to represent this group of species because it honors a Mexican botanist, Dr. F.G. Medrano, which seems appropriate for this group of primarily Mexican species.

1. Medranoa johnstonii (G.L. Nesom) G.L. Nesom, comb. nov. *Neonesomia johnstonii* (G.L. Nesom) Urbatsch & R.P. Roberts; *Xylothamia johnstonii* G.L. Nesom, Sida 14:110. 1990.

2. Medranoa parrasana (S.F. Blake) Urbatsch & R.P. Roberts, Sida 21:255. 2004. *Ericameria parrasana* S.F. Blake; *Haplopappus parrasanus* (S.F. Blake) S.F. Blake; *Xylothamia parrasana* (S.F. Blake) G.L. Nesom.

3. Medranoa palmeri (A. Gray) G.L. Nesom, comb. nov. *Aster palmeri* A. Gray, Proc. Amer. Acad. Arts 17:209. 1882.; *Ericameria austrotexana* M.C. Johnston (non *Ericameria palmeri* (A. Gray) H.M. Hall); *Neonesomia palmeri* (A. Gray) Urbatsch & R.P. Roberts; *Xylothamia palmeri* (A. Gray) G.L. Nesom.

4. Medranoa purpusii (Brandeg.) G.L. Nesom, comb. nov. *Ericameria purpusii* Brandeg., Univ. Calif. Publ. Bot. 4:191. 1911; *Chihuahuana purpusii* (Brandeg.) Urbatsch & R.P. Roberts; *Haplopappus [Aplopappus] purpusii* (Brandeg.) S.F. Blake; *Xylothamia purpusii* (Brandeg.) G.L. Nesom.

5. Medranoa pseudobaccharis (S.F. Blake) G.L. Nesom, comb. nov. *Haplopappus pseudobaccharis* S.F. Blake, J. Washington Acad. Sci. 40:47. 1950; *Ericameria pseudobaccharis* (S.F. Blake) Urbatsch; *Xylothamia pseudobaccharis* (S.F. Blake) G.L. Nesom; *Xylovirgata pseudobaccharis* (S.F. Blake) Urbatsch & R.P. Roberts.

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Urbatsch, L.E. and R.P. Roberts. 2004. New combinations in the genus *Gundlachia* and four new genera of Astereae (Asteraceae) from northern Mexico and the southern United States. Sida 21:243–257.